ELSEVIER

Deep-Sea Research II 51 (2004) 1397–1409

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean

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Accepted 18 June 2004
Available online 25 September 2004

Abstract

Baleen whales are an important group of predators on Antarctic krill in the Southern Ocean. During the CCAMLR 2000 Survey to estimate the biomass and distribution of Antarctic krill, International Whaling Commission observers carried out a visual line transect survey to estimate the number of baleen whales occurring in the survey area. This paper reviews techniques used to estimate krill consumption by baleen whales and in combination with estimates of whale abundance estimates of krill consumption are generated for the South Atlantic sector of the Southern Ocean. This survey estimates that the present populations of whales feeding in this region are likely to consume approximately 1.6 million tonnes, but possibly up to as much as 2.7 million tonnes of krill within the summer season. Although this only represents 4–6% of the estimated krill biomass in the region (and probably less than this percentage of the total annual krill production), the depleted numbers of baleen whales resulting from past or current whaling activities should be taken into account when setting quotas for the commercial exploitation of krill if there is to be a recovery to pre-exploitation biomass levels of baleen whales.
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1. Introduction

The International Whaling Commission (IWC) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) share an interest in the feeding ecology of Antarctic baleen whales. The IWC has for many years been interested in the feeding ecology of baleen whales, especially in the Southern Ocean, as part of its efforts to place its management decisions within an ecosystem context. CCAMLR

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0967-0645/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.dsr2.2004.06.008

has an ongoing interest in the amount of krill consumed in the Southern Ocean by all krill predators, including baleen whales, because it explicitly considers predator requirements in setting quotas for commercial exploitation of krill. This shared interest led to the first collaborative field program, the CCAMLR 2000 Survey, between the two commissions' scientific committees in January and February 2000. The primary objective of the survey was to obtain an up-to-date estimate of krill biomass for the region to use in setting a precautionary catch limit for the commercial krill fishery (Hewitt et al., 2002, 2004; Watkins et al., 2004), although both commissions recognized this as an ideal opportunity to couple whale sighting surveys with the krill surveys.

This paper estimates krill consumption by the more abundant baleen whale species in the South Atlantic region of the Southern Ocean for the 2000 summer feeding season. The consumption estimates are based on whale abundance estimates (Hedley et al., 2001) derived from line transect sighting surveys conducted by teams from the IWC Scientific Committee onboard the RRS *James Clark Ross*, the RV *Yuzhmorgeologiya,* and the RV *Kaiyo Maru* during the CCAMLR 2000 Survey. The abundance estimates are used in conjunction with estimated prey consumption rates to estimate krill biomass consumed within the study area, and its energy content. Because direct estimation of consumption rates is not possible, this paper first reviews indirect methods previously employed, then applies what is considered to be a simplified but sound approach.

2. Data and methods

2.1. CCAMLR 2000 overview

Four ships participated in the CCAMLR 2000 Survey, three of these (RRS *James Clark Ross*, RV *Kaiyo Maru* and RV *Yuzhmorgeologiya*) surveyed two sets of interleaved parallel transects across the Scotia Sea (Scotia Sea stratum) and northwest of the Antarctic Peninsula (Antarctic Peninsula stratum). The fourth ship (RV *Atlantida*) surveyed transects in the eastern Scotia Sea and around the South Sandwich Islands. On each ship acoustic transects were run continuously during the hours of daylight apart from a stop to carry out a CTD cast and a net haul in a three-hour period prior to local midday. No acoustic transecting was undertaken at night. Full details of the krill sampling design and rationale are reported by Watkins et al. (2004).

2.2. Cetacean data collection

An IWC workshop was held in Edinburgh in March 1999 (IWC, 1999) to consider the design and analysis of the cetacean component of multidisciplinary surveys, and in particular how cetacean sightings data should be collected during SOWER-2000 (Southern Ocean Whale Ecosystem Research-2000, the IWC designation for the CCAMLR 2000 Survey). It concluded that where possible, cetacean observations should be made using a two-platform asymmetric survey protocol (referred to throughout this paper as BT mode and fully described in Buckland and Turnock, 1992). As noted in the workshop report (IWC, 1999), BT mode potentially enables more precise and accurate estimates of whale density compared to estimates derived from a single observer team, however, significantly more observers are required to operate in BT mode. Owing to logistic constraints it was not possible to accommodate IWC teams large enough to operate in continuous BT mode or even to have the same number of observers on each ship. There were six IWC observers on the *Yuzhmorgeologiya*, four on the *James Clark Ross*, and two on the *Kaiyo Maru*. Participation of the *Atlantida* was finalized relatively late in the planning process and this ship did not carry any cetacean observers. Because of the differing number of cetacean observers, the survey protocols differed on each vessel, but were standardized as far as possible.

Two survey modes were used during the CCAMLR 2000 Survey. Primary mode used one observation team of three observers on the *Yuzhmorgeologiya*, and one team of two observers on the *James Clark Ross* and *Kaiyo Maru*. BT mode used two independent teams operating at the same time. Because of the extra personnel required to operate in BT mode, this was only used on the

Yuzhmorgeologiya and the *James Clark Ross,* where effort was divided between Primary and BT modes according to weather conditions and to incorporate rest periods and meal breaks.

In Primary mode, observers with 7×50 binoculars searched for cetaceans across a field of view from directly ahead to at least 90° on the beam. To obtain some protection from weather the observers worked from the bridge wings or similar locations providing protected but minimally obstructed views. In BT mode, four observers searched simultaneously from two independent observation points—the Primary platform and the Tracking platform. Two observers on the Primary platform searched for cetaceans as described for Primary mode, and were not informed of sightings made from the Tracking platform. The Tracking platform comprised a 'Recorder' and a 'Tracker'. The Tracker searched for cetaceans using Fujinon 25×150 binoculars (known as 'Big Eyes') which were mounted on a tilting, rotating cradle fixed to the deck. When not entering data, the Recorder also searched with 7×50 binoculars. The Recorder judged whether sightings were new sightings from either platform or 'duplicates' (whales seen first by the Tracking team and then seen subsequently by the Primary team).

Data from a cetacean survey are most useful when the survey has been conducted in good weather. In such a case, the absence of sightings can be more readily attributed to an absence of animals, rather than a failure to detect their presence. In parts of the Southern Ocean, good survey conditions occur intermittently and are quite uncommon, meaning observations must be made under a range of conditions. Acceptable survey conditions were defined using guidelines from IWC IDCR/SOWER (International Decade of Cetacean Research/Southern Ocean Whale and Ecosystem Research) surveys as follows:

- Wind speed is less than 20 knots.
- Beaufort sea state is less than 6.
- The distance at which a minke whale blow might be visible is at least 1.5 nautical miles.

In practice, the decision as to whether survey conditions were acceptable was left to the senior cetacean scientist on each vessel. Extremely poor conditions were encountered, particularly in the first half of the survey in the Scotia Sea region. However, in an attempt to obtain at least some data for the eastern half of the Scotia Sea, whale observations were conducted up to Beaufort sea state 7 and in thick fog, which limited visibility to just 0.5 nm. The motivation for collecting these data was primarily to provide insights into cetacean-prey-habitat relationships. It was recognized that such data were probably of substantially less use in providing data for analyses aimed primarily at estimating abundance.

2.3. Whale abundance estimates

Estimation of abundance was based on distance sampling (e.g., Buckland et al., 1993) using Distance 3.5 (Thomas et al., 1998). Thus, the cruise was designed to sample distance to whales along a transect, and line-transect methods were used to estimate the density of schools. For each type of whale, abundance N was estimated by multiplying estimated school density by expected school size $E(S)$ and area A in each stratum, using the equation:

$$\hat{N} = \frac{nf(0)}{2L} E(S)A,$$

where n is the number of sightings, L the search effort (transect length), and $f(0)$ the estimated value of the sighting probability density function evaluated at zero distance from the trackline. Details, including data stratification and estimation of the detection function, $g(x)$, can be found in Hedley et al. (2001). This paper reports abundance estimates for the following, most frequently observed categories of baleen whales:

- Minke whales, *Balaenoptera bonaerensis* (including 'like minke' and 'undetermined minke').
- Humpback whales, Megaptera *novaengliae*.
- Fin whales, *B. physalus* (including 'like *B. physalus*').
- Right whales, *Eubalaena australis* (including 'like *E. australis*').
- Large baleen whales (including the humpback, fin, and right whale categories above, plus

'unidentified large baleen whale', 'like *B. musculus*' (blue whale), *B. borealis* (sei whale) and 'like *B. borealis*'.

Sightings recorded as 'unidentified large whale' were not included in the analysis, as these potentially include sperm whales, which do not consume krill.

2.4. Review of methods to estimate krill consumption by whales

Prey consumption by living baleen whales can only be estimated indirectly. Past studies have used various approaches to this problem, but all required assumptions that to date have not been testable for one or more key parameters. Instead, it has been necessary to posit logical limits from incomplete information in order to complete the estimation process. Consequently this paper presents a range of values for consumption rates and amounts, rather than point estimates with ill-defined precision and accuracy. The previously published methods for the larger baleen whales have been modified slightly using currently available information. The best estimates are available for minke whales and this paper uses published values for consumption rates for four age-sex categories.

2.4.1. Direct methods

The most direct method to estimate consumption by baleen whales has included weighing the stomach contents of whales killed for commercial or research whaling (e.g., Bushuev, 1986; Ichii and Kato, 1991; Klumov, 1963; Ohsumi, 1979). To estimate daily, seasonal, and annual consumption rates assumptions must be made about how frequently the whales fill their stomachs. In order to estimate daily rates, Tamura et al. (1997) applied a method developed by Miura (1969; not seen but cited by Tamura et al., 1997) based on diurnal change in forestomach content mass. While limited, this is the most quantitatively defensible approach applied to date for baleen whales. This produced estimates of 3.2–3.5% of body weight per day. However, even this method relied on an assumption of a key rate parameter, in this case Bushuev's (1986) view that food takes five hours to pass through the forestomach. Tamura et al. (1997) then applied two other, energetic-based approaches, using an extrapolation of standard metabolic rates and body mass increase during the summer feeding season. All three methods, as applied by these authors, produced estimates of similar magnitude, ranging from 3.2% to 4.1% per day. Lacking a clear criterion to distinguish between the three estimates, Tamura et al. (1997) simply averaged the three values to estimate daily consumption rates for four age/sex classes (Table 1).

Sergeant (1969) measured the daily food intake of captive Delphinoidea to derive an allometric equation based on heart mass to body mass ratio. This equation was modified by Innes et al. (1986) as $I = 0.42 M^{0.67}$ (where M is the mass of the whale in kg and I is the daily ingestion rate given as $\mathrm{kg\,d^{-1}}$). Some workers have applied this model to estimate daily rates for the larger whales (e.g., Armstrong and Siegfried, 1991; Sigurjonsson and

Table 1
Population structure, body weight, and consumption rates of Southern Ocean minke whales in the Central Pacific sector (IWC area IV) (Tamura et al., 1997)

Sex	Maturity stage	Body weight (kg)	Population (%)	Consumption %	Consumption $\mathrm{kg\,d^{-1}}$
M	Immature	3000	9.13	3.8	114.0
	Mature	6900	41.97	3.4	234.6
F	Immature	3900	20.44	3.7	144.3
	Mature	8100	28.46	3.7	299.7

Body weights and population percentages are for whales sampled without size selection during the JARPA program. Consumption rates, given as percentage body weight per day, are the average of results of three independent methods.

Vikingsson, 1999); however, it is questionable whether such extrapolation is valid far beyond the range of body sizes used in Sergeant's original derivation. This relationship is examined further below, and modified slightly for application to the larger baleen whales observed during the CCAMLR 2000 Survey.

2.4.2. Energy budget studies

Another major category of estimates is that derived from studies of cetacean energy budgets. These methods are based on estimates and assumptions regarding basal metabolic rate, growth, reproduction, migratory and other movements, and fat deposition for winter. The basic energy budget studies have produced important insights into cetacean bioenergetics, but extending them to estimate daily consumption rates involves a number of difficulties. Such an extension requires a number of guesses for components of the energetic system that have not been measured and perhaps never could be measured directly. The primary examples are reviewed below. Thus, energetic-based methods are likely to produce less reliable estimates of consumption rates because of the many important but unmeasured components.

Hinga (1979) analyzed cetacean respiration and feeding data collected for captive, small whales (100–6000 kg in weight) and applied the outcome to fin whales by scaling to basal metabolic rate. With the addition of Brodie's (1975) energy storage calculation, Hinga (1979) estimated that fin whales consume 700–1000 $kg\,d^{-1}$ (1.5–2% of body mass) during their 120-day summer feeding period in Antarctic waters.

Lockyer (1981a) calculated energy required for growth comparing different previously published metabolic rates, and later incorporated a review of data on stomach contents of Balaenopterids (Lockyer, 1981b). Utilizing Klumov's (1963) estimate for daily intake, she concluded that baleen whales require 30–40 $g\,kg^{-1}$ body weight per day (3.0–4.0%) during their 120-day summer feeding period in the Antarctic. This rate accounts for 83% of their annual food intake. This study re-examined Klumov's (1963) analysis and found that the estimate of 30–40 $g\,kg^{-1}\,d^{-1}$ was based on a subjective evaluation (Klumov, 1961) of data from a number of sources (many unreferenced), including data on humans and other non-cetacean species. Consequently, it is felt that the range of 30–40 $g\,kg^{-1}\,d^{-1}$ proposed by Klumov (1961) does not provide a sound basis for extrapolation.

Armstrong and Siegfried (1991) estimated the total energy requirements of minke whales in the Antarctic using both stomach capacity/ingestion rates and the energy budget approach (which they termed 'respiratory allometry'). These authors regarded their stomach capacity results as less reliable than their energy budget results, owing to a lack of knowledge about feeding rates and degree of stomach emptying/filling. However, their final conclusion, based on both stomach capacity information and energetics, was that minke whales on the summer feeding grounds consume between 5% and 7% of their body mass per day. This is considerably higher than the more direct and quantitative findings (3.2–3.5%) of Tamura et al. (1997), who commented that Armstrong and Siegfried's food consumption rates appeared to be overestimates.

Sigurjonsson and Vikingsson (1999) employed both feeding rates of captive cetaceans (using the formula of Innes et al., 1986), and energy budgets based on the relationship between physiological parameters and body weight, to calculate ingestion rates for balaenopterids in the North Atlantic near Iceland. Values for daily rates estimated by the two methods were not dramatically different (although the differences increased with increasing body size). Following Lockyer's (1981a) estimate that Southern Hemisphere balaenopterids consumed 83% of total annual intake during summer, they scaled summer daily rates to ten times the rates for the rest of the year (summer rate = 2.53 d, rest of year daily rate = 0.253 d). This gave daily consumption rates during summer of over 7% body mass per day for minke whales and 3.9% per day for humpback whales. As with the rates estimated by Armstrong and Siegfried (1991), their estimate of over 7% for minke whales is more than twice the range of 3.2–3.5% per day estimated by Tamura et al. (1997), and so is probably biased upward. As with most other estimates of daily feeding rate, there are a number of assumptions behind these estimates that are based on very little data. Again, for minke whales the present authors regard the more direct and quantitative estimates of Tamura et al. (1997) to be more reliable.

Leaper and Lavigne (2001) conducted an in depth review of studies that estimated daily rates of prey consumption by cetaceans, concurrent although independent of the present study. They found that all the studies calculated daily ingestion rates as a function of the cetaceans' body mass using the following basic model: $I=AM^{B}$; where A and B are estimated from various data sources. The most influential parameter in this equation is B and Leaper and Lavigne (2001) concluded that high values of B close to 1 should be rejected. For filter-feeding baleen whales values for B of 0.67 or less have the strongest theoretical basis, and were most consistent with daily consumption amounts estimated from right whales feeding in the Northwest Atlantic (Leaper and Lavigne, 2001). Based on these conclusions, the model produced by Innes et al. (1986) which used a B value of 0.67 was revised in the present study. Their estimate of daily ingestion by blue whales was set as the maximum value in this study and the lower end of the present model was anchored to fit the four data points for minke whales produced by Tamura et al. (1997).

2.5. Krill consumption by minke whales during the CCAMLR 2000 Survey

This study applied the daily consumption rate estimates of Tamura et al. (1997) directly for minke whales. Their estimates of body weight and population proportions for adults and juveniles, males and females were also used to estimate the amount of krill consumed by each of the four age/sex classes during the summer feeding season. This was achieved by multiplying the daily rates by 120 (following Lockyer, 1981a, b estimate of a 120-day feeding season) to estimate total rates for the feeding season. These seasonal rates were then multiplied by the estimates of minke whale abundance for the CCAMLR 2000 Survey area (Hedley et al., 2001), proportionately divided between the four age/sex classes.

2.6. Krill consumption by other baleen whales during the CCAMLR 2000 Survey

Lacking more direct estimates as exist for minke whales, an allometric model (approximated by an exponential function, as used by Sergeant, 1969, and Innes et al., 1986) was regarded as the most appropriate for estimating consumption as a function of body size, and so this study used the same basic model, but estimated new parameters as follows. The models were fitted to the four Tamura et al. (1997) estimates for minke whales, which the present authors consider to be the best representation of the lower end of the size range for baleen whales, and anchored the fit to a range of values for blue whales at the upper end of the size range. Given the general assumption of lower rates for larger animals, daily rates of more than 3% for blue whales, with average body weights near 85,000 kg (Laws, 1977), are considered very unlikely given the 3.2–3.5% estimated for minke whales with body weights ranging from 3000 to 8100 kg (Table 1). Consequently, four models were produced during this study fitted to the four minke whale points at the lower end and to maxima using (1) the ingestion for blue whales from the model of Innes et al. (1986); and, blue whale consumption rates of (2) 2% of body mass, (3) 2.5% of body mass, and (4) 3% of body mass, to represent a likely range of allometric models. This paper reports estimates from each of the four models for baleen whale species other than minke whales, based on their average body weights as reported by Laws (1977). These models represent first order approximations for the range and shape of the inter-specific relationship between daily consumption and body size for baleen whales.

As for minke whales, the daily rates were scaled up to total rates for the feeding season by multiplying by 120 and then multiplied by the estimated abundance for the CCAMLR 2000 Survey area.

2.7. Species composition and energy content of prey consumed

In this study the simplifying assumption is made that all prey consumed by baleen whales in the study area are krill. This is defensible for minke and humpback whales, but right and fin whales are also reported to consume copepods and small fishes, although this apparently varies by time and location (Kawamura, 1978). Clarke (1980) reported a mean caloric value of approximately 1100 kcal kg^{-1} for Antarctic krill (*Euphausia superba*) in February near South Georgia. This value was used here to convert mass of krill consumed to energy content.

3. Results

3.1. Whale distribution and abundance estimates

A total of 730 cetacean sightings were recorded during the CCAMLR 2000 Survey, comprising 1753 individuals. Of these, 682 sightings were made during acceptable sighting conditions and on a predefined transect. An additional 48 sightings were made during transits to and from the study area. By species, the following groups were observed during acceptable conditions and so may be used in abundance estimation: 112 minke, 181 humpback, 56 fin, 24 right, 7 sei, 1 blue, and 91 unidentified large baleen whale groups. Full details can be found in Hedley et al. (2001).

Fig. 1 shows whale sighting localities, together with transect lines completed during periods of acceptable sighting conditions. All but one of the right whale sightings were made in the Scotia Sea, most occurring just north of South Georgia. Minke whales were seen patchily throughout the survey area, with a modestly greater estimated abundance in the Antarctic Peninsula stratum (Table 2). Fin whales were encountered in both strata, with estimated abundance in the Scotia Sea about twice the abundance along the Antarctic Peninsula (Table 2). Humpback whales were relatively abundant in the northwest part of the Scotia Sea, but even more so along the Antarctic Peninsula, where they were frequently encountered in the more nearshore areas. Minke whales were the most abundant baleen whale in the study area 18,125 (coefficient of variation, CV = 28.28), followed by humpback whales, fin whales, and right whales (Table 2). The combined total for large baleen whales, excluding minke whales but including blue and sei whales, was 17,944 (CV = 19.37).

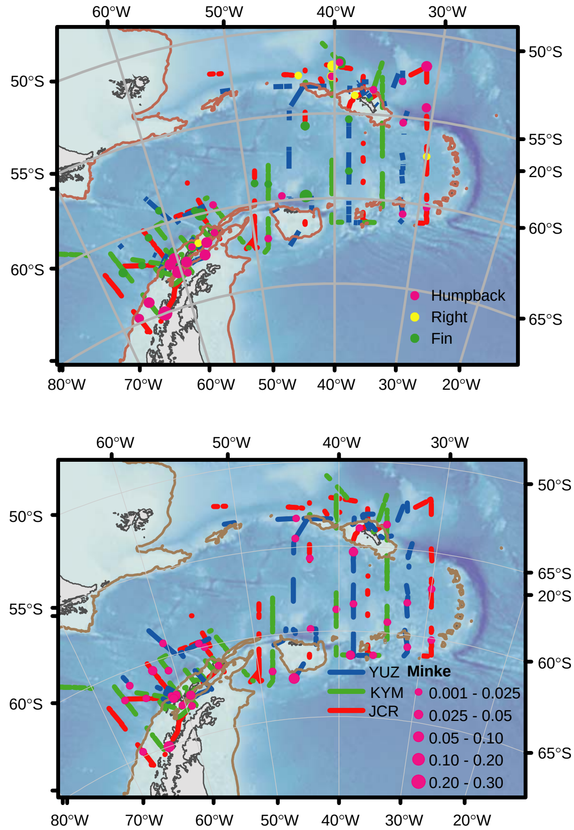

Fig. 1. Cruise tracks of the RV *Yuzhmorgeologiya* (YUZ), RV *Kaiyo Maru* (KYM), and RRS *James Clark Ross* (JCR) in the South Atlantic sector of the Southern Ocean. Upper panel shows daily encounter rates for humpback, right, and fin whales. Lower panel shows daily encounter rates for minke whales.

There were too few sightings of blue and sei whales to estimate their abundance separately and so a combined estimate has been produced for all large baleen whales (Table 2). This was done to allow a more complete account of the occurrence of this group of krill-eating species for use in estimation of prey consumption. Full details, including sample sizes and model forms, are reported by Hedley et al. (2001).

Table 2
Abundance of baleen whales within the CCAMLR 2000 Survey area during January and February 2000 (Hedley et al., 2001)

Species	Area	Abundance	(CV %)
Minke	SS	10,730	(31.36)
	AP	7395	(35.98)
	Full area	18,125	(28.28)
Humpback	SS	2493	(54.95)
	AP	6991	(32.41)
	Full area	9484	(27.92)
Fin	SS	3180	(56.64)
	AP	1492	(57.08)
	Full area	4672	(42.37)
Right	SS	1712	(62.98)
	AP	43	(185.34)
	Full area	1755	(61.67)
Large baleen[a]	SS	9157	(27.08)
	AP	8787	(24.72)
	Full area	17,944	(19.37)

SS: Scotia Sea stratum; AP: Antarctic Peninsula stratum.
[a]Includes humpback, fin, right, blue and sei whales.

3.2. Krill consumption

3.2.1. Minke whales

Proportions of the minke whale population within four categories (male or female and immature or mature) are given in Table 1, together with average body weights and daily consumption rates for each category from Tamura et al. (1997). This study assumes that minke whales in the South Atlantic sector of the Southern Ocean shared these characteristics with those of the central Pacific sector as reported by Tamura et al. (1997). Total consumption within the Scotia Sea stratum by minke whales was estimated to be more than 287×10^6 kg, or $316{,}782 \times 10^6$ kcal. Estimates for the Antarctic Peninsula stratum are $198{,}921 \times 10^3$ kg or $218{,}813 \times 10^6$ kcal. Total consumption of krill by minke whales within the study area was estimated to be $486{,}905 \times 10^3$ kg or $535{,}595 \times 10^6$ kcal. Subtotals for the four age and sex categories are given in Table 3.

3.2.2. Other baleen whales

3.2.2.1. Consumption rates as a function of body mass. The exponential model parameters for the revised form of the Innes model, fit to the four minke whale points at the low end of the size range and to the maximum for blue whales from the original Innes et al. (1986) model were: $I=1.66M^{0.559}$. Other models worth considering were those with maxima of 2% ($I=0.256M^{0.775}$), 2.5% ($I=0.123M^{0.859}$), and 3%, ($I=0.067M^{0.929}$). Plots of these four models are shown in Fig. 2 together with the original Innes et al. (1986) model ($I=0.42M^{0.67}$). The present authors regard the revised Innes model to be the most appropriate model form, and used results from that model as the basis of the estimates of consumption presented here. However, given the overall uncertainty involved in estimating daily consumption by baleen whales, the results based on other models are also shown to allow evaluation of the range of possible consumption rates.

Table 4 shows daily consumption rates arising from the four new models for humpback, fin, right, sei, and blue whales. The Innes revised model predicts daily consumption rates of 497 kg for humpback whales, 693 kg for fin whales, 748 kg for right whales. Applying these rates to the estimated abundance by species (Table 2) and multiplying by 120 gives the seasonal total consumption estimates shown in Table 5. With the Innes revised model, humpback whales are estimated to consume $565{,}886 \times 10^3$ kg, fin whales $388{,}561 \times 10^3$ kg, right whales $157{,}501 \times 10^3$ kg, comprising a total of $1{,}111{,}948 \times 10^3$ kg (1.11 million tonnes) and $1{,}223{,}143 \times 10^6$ kcal. These totals increase to $2{,}209{,}121 \times 10^3$ kg (2.21 million tonnes) and $2{,}430{,}033 \times 10^6$ kcal for the 3% max model.

3.2.3. Combined total consumption by baleen whales

With the Innes revised model, the total mass of krill consumed by minke, humpback, fin and right whales in the study area during the 120-day summer season was estimated at $1{,}598{,}853 \times 10^3$ kg (1.6 million tonnes) and $1{,}758{,}738 \times 10^6$ kcal. Using the 3% maximum rate model yields estimates of $2{,}696{,}025 \times 10^3$ kg (2.69 million tonnes) and $2{,}965{,}628 \times 10^6$ kcal.

This paper focuses on estimates for minke, fin, humpback, and right whales because these species were present in sufficient numbers to allow

Table 3
Minke whale krill consumption during an annual feeding season of 120 days within the CCAMLR2000 Survey area in the western South Atlantic sector of the Southern Ocean

Area	Sex	Maturity state	Abundance	Consumption (10^3 kg)	Energy content (10^6 kcal)
SS	M	Immature	980	13402	14742
		Mature	4503	126779	139457
	F	Immature	2193	37978	41775
		Mature	3054	109825	120808
		SS subtotals		*287984*	*316782*
AP	M	Immature	675	9234	10157
		Mature	3104	87838	96621
	F	Immature	1512	26181	28800
		Mature	2104	75668	83235
		AP subtotals		*198921*	*218813*
Full Area	M	Immature	1655	22636	24899
		Mature	7607	214617	236078
	F	Immature	3705	64159	70575
		Mature	5158	185493	204043
Totals			18125	486905	535595

Abundance is partitioned from the estimates in Table 2 and the population proportions in Table 1. Totals are for the full study area, all age/sex classes combined.
SS: Scotia Sea stratum; AP: Antarctic Peninsula stratum

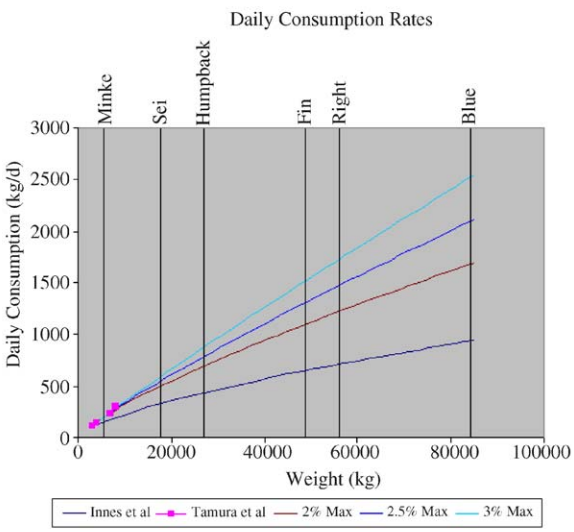

Fig. 2. Daily consumption rates as a function of body weight for the model of Innes et al. (1986) and three new models using the same functional form ($I = aMb$, where I is daily consumption rate and M is body weight), fit as described in the text.

reasonably precise estimates of abundance, and therefore consumption. However, it is possible to extend these results to generate crude estimates of abundance for the rarely sighted sei and blue whales. This is achieved by pro-rating from the combined baleen whale species estimate (Table 1) using the proportions of sei and blue whales encountered (2.4% and 0.2% of all sightings) to generate estimates of roughly 420 sei and 35 blue whales. Using the Innes revised model their consumption of krill is estimated to be approximately $16{,}620 \times 10^3$ and 3948×10^3 kg, respectively. Adding the estimates for sei and blue whales slightly increased the combined total estimates of consumption by baleen whales, to $1{,}619{,}421 \times 10^3$ kg and $1{,}788{,}602 \times 10^6$ kcal using the Innes revised model; and to $2{,}716{,}594 \times 10^3$ kg and $2{,}988{,}253 \times 10^6$ kcal using the 3% max model.

4. Discussion

The abundance estimates by Hedley et al. (2001) were made using fully accepted methods for estimating absolute abundance. They are however somewhat imprecise, having CVs ranging from about 28% for minke and humpback whales to

Table 4
Body weight (M) and individual daily consumption rate (I) for Southern Ocean humpback, fin, right, sei, and blue whales

Species	Body weight (M) (kg)	Innes et al. (kg)	Innes revised (kg)	2% Max (kg)	2.5% Max (kg)	3% Max (kg)
Humpback	26,924	390.34	497.23	694.38	785.95	874.33
Fin	48,768	581.17	693.07	1100.38	1309.22	1518.28
Right	55,880	636.67	747.87	1222.82	1471.63	1722.96
Sei	17,780	295.60	394.29	503.43	550.30	594.65
Blue	84,328	838.78	941.30	1682.16	2095.63	2525.24

Consumption rates are estimated from three allometric models of the form $I = aM^{b}$ relating daily consumption to body weight. The three models in common use values for minke whales from Table 2, but fit to maximum rates of 2, 2.5, or 3% for blue whales, the largest species.

62% for right whales. No estimates were made for sei or blue whales due to the low numbers of sightings recorded. The relatively high CVs reflect the generally poor sighting conditions encountered and therefore fewer than anticipated track miles completed in conditions acceptable for detecting whales. The abundance CVs were not used when estimating krill consumption, because the krill consumption rates were not statistically based, but these large coefficients of variation must be kept in mind when evaluating the final estimates of mass and energy consumed by the region's baleen whales.

The present method for estimating daily consumption rates for the larger baleen whales should be a modest improvement over existing methods, but still provides only crude ranges, and could probably be improved by a more thorough review of available data and a statistically based modeling effort. A Bayesian approach might prove particularly effective.

A simplifying assumption made here, as in previous studies to estimate krill consumption by baleen whales, is that all whales in the populations studied spent all 120 days of the possible southern summer feeding season within the study area. This is probably a reasonable assumption for some species, e.g. humpback whales, but not for all. Some species such as minke and blue whales are thought to migrate to the ice edge zone to feed, and so may not spend the entire summer in the study area. It is possible that some individuals had already migrated through the study area to the ice edge before the surveys began, and so would have been missed. They are thought to migrate in early summer (December) to the area near the ice edge where krill are aggregated in such a way as to increase the foraging success of these two species, but later in summer (January–March) are to be found foraging both near the ice edge and farther off the ice edge in association with topographical features such as shelf breaks, and may also be found near hydrographic fronts (Ichii, 1990). This implies that some krill aggregate near the ice edge, outside the area studied during CCAMLR 2000, and so the krill biomass estimates may be negatively biased to some extent.

During this study it was assumed that all baleen whales observed were foraging solely on krill. This simplifying assumption is reasonable for most species, however some whales may have been foraging on other prey such as copepods or fishes. This will have biased the present estimates of krill consumption upward, but probably by only a small amount.

The consumption estimates could be further biased, either up or down, depending on the accuracy of Lockyer's (1981a) conclusion that 83% of the annual energy intake for Southern Ocean cetaceans occurs during the 120-day feeding season. This value was based on her estimate for the total energy requirements of baleen whales for growth and was the basis for many subsequent estimates of cetacean consumption.

Hewitt et al. (2002, 2004) estimated a standing stock or biomass of approximately 44 million tonnes of krill in the study area. The present study estimated a seasonal total consumption by whales

Table 5
Humpback, fin, and right whale consumption of krill during the 2000 summer feeding season within the CCAMLR 2000 Survey area in the western South Atlantic sector of the Southern Ocean

Species	Body mass	Area	Abundance	Innes revised		2% Max		2.5% Max		3% Max	
				Consumption (10^3 kg)	Energy content (10^6 kcal)	Consumption (10^3 kg)	Energy content (10^6 kcal)	Consumption (10^3 kg)	Energy content (10^6 kcal)	Consumption (10^3 kg)	Energy content (10^6 kcal)
Humpback	26,924	SS	2493	148,751	163,626	207,731	228,504	235,125	258,637	261,564	287,720
		AP	6991	417,135	458,849	582,531	640,784	659,349	725,284	733,491	806,841
		Total	9484	565,886	622,475	790,262	869,288	894,474	983,922	995,055	1,094,561
Fin	48,768	SS	3180	264,475	290,922	419,907	461,897	499,599	549,559	579,376	637,314
		AP	1492	124,087	136,495	197,013	216,714	234,403	257,843	271,833	299,016
		Total	4672	388,561	427,417	616,920	678,612	734,002	807,402	851,209	936,330
Right	55,880	SS	1712	153,642	169,006	251,217	276,338	302,331	332,565	353,966	389,362
		AP	43	3859	4245	6310	6941	7594	8353	8890	9780
		Total	1755	157,501	173,251	257,527	283,279	309,925	340,918	362,856	399,142
Totals			15911	1,111,948	1,223,143	1,664,708	1,831,179	1,938,401	2,132,241	2,209,121	2,430,033

Estimates are presented for three different models of daily consumption as a function of body mass. The three models differ by the maximum daily rate assumed for the largest species (blue whales); 2%, 2.5%, or 3% of body mass per day.
SS: Scotia Sea stratum; AP: Antarctic Peninsula stratum.

of between 1.6 and 2.7 million tonnes. This range is approximately 4–6% of the standing stock. Hewitt et al. (2004) did not estimate total production, which would be larger than the standing stock (Siegel and Nicol, 2000; Voronina, 1983). Therefore, excluding issues of precision, it is likely that baleen whales at their current population levels require somewhat less than 6% of total krill production. However, the present estimates are clearly of low precision, and therefore could be low by as much as 100%.

Baleen whales are not the only krill consumers in the Antarctic; krill constitute approximately 82% of the diet of seabirds and 54% of the diet of pinnipeds (Croxall et al., 1985). Croxall et al. (1985) evaluated consumption by seabirds and pinnipeds in the Scotia Sea region of the Antarctic, extending to the base of the Antarctic Peninsula on the western side, and including South Georgia and other satellite islands to the northeast. The main krill consumers in this region are crabeater seals, macaroni penguins, and chinstrap penguins; with annual krill consumption by all seabirds and pinnipeds in this area totaling an estimated 16 million tonnes (Croxall et al., 1985). Although they acknowledge that this value is probably an overestimate, this is quite significant since it is ten times greater than the best estimate of krill consumption by baleen whales (1.6 million tonnes; see Section 3.2.3) using the Innes revised model. It is important to note that the area surveyed in this study is not identical to that surveyed during CCAMLR 2000, although it is likely to be sufficiently similar to be suitable for a general comparison of krill consumption by seabirds and pinnipeds to that of whales. Another factor potentially limiting such a comparison is major changes in abundance of seabird and pinniped populations between the CCAMLR 2000 survey and the time at which this paper was written.

All species of baleen whale in this region are depleted to some extent from past or current whaling activities (e.g. Gambell, 1999) and therefore will require additional prey resources to achieve any level of recovery relative to their pre-exploitation level. This paper has consciously avoided the debate on whether a ‘krill surplus’ resulted from the depletion of baleen whales, and the extent to which the krill-predator systems have been modified. However, it must be emphasized that any quotas set for commercial exploitation of krill should be defined with substantially larger values for baleen whale consumption than those estimated here for currently depleted whale populations.

Acknowledgements

We thank the Scientific Committees of both the IWC and CCAMLR for encouraging and supporting this collaboration, the whale observers (Simon Berrow, James Cotton, Mike force, Russel Leaper, Paula Olson, Robert Pitman, Todd Pusser, Koen Van Waerebeek, and Amy Williams) the officers and crew of the RV *Yuzhmorgeologiya*, the RSS *James Clark Ross* and the RV *Kaiyo Maru*. Funding for the whale component of the joint research effort was generously provided by the IWC and the UK and USA.

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